

MINI REVIEW

The algae energy pathway: An emerging mechanism for energy transfer in northern peatlands

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Abstract

1. Microbial photoautotrophs (i.e. algae) are increasingly recognized for their importance to the global carbon cycle. This is especially true in carbon-accumulating ecosystems such as peatlands, where the capacity for carbon storage is substantial but also vulnerable to climate change. The potential for peatlands to store carbon in the future hinges largely on the magnitude of microbially mediated carbon cycling.
2. Warmer temperatures are promoting the release of carbon dioxide (CO₂) stored through traditional detrital energy pathways (i.e. peat formation), but climate change is also facilitating the expansion of aquatic habitat across the boreal landscape and increasing nutrient availability, thereby promoting carbon uptake through an algal energy pathway.
3. Algae provide a labile source of energy to both the microbial loop and higher trophic levels, making this new energy pathway susceptible to top-down regulation.
4. *Synthesis.* We synthesized research from northern peatlands showing how recent environmental conditions set in place by climate change can govern CO₂ emissions by regulating the composition of microbes on peat surface layers. We highlight conditions such as expanding areas of aquatic habitat and enhanced nutrient cycling that favour algal-mediated carbon uptake and demonstrate how the presence or absence of an algal energy pathway can determine the direction of peatland carbon flux.

KEYWORDS

bacteria, carbon cycling, decomposition, dissolved organic carbon, global change ecology, photoautotrophs, resource subsidies, wetland drying

1 | BACKGROUND

The transfer of energy from primary producers to heterotrophs is a fundamental process driving ecosystem functioning

(Lindeman, 1942; Odum, 1956). Ecologists typically characterize ecosystems as having either green or brown energy pathways, highlighting whether living primary production or detritus, respectively, is the primary driver of energy transfer (Hairston

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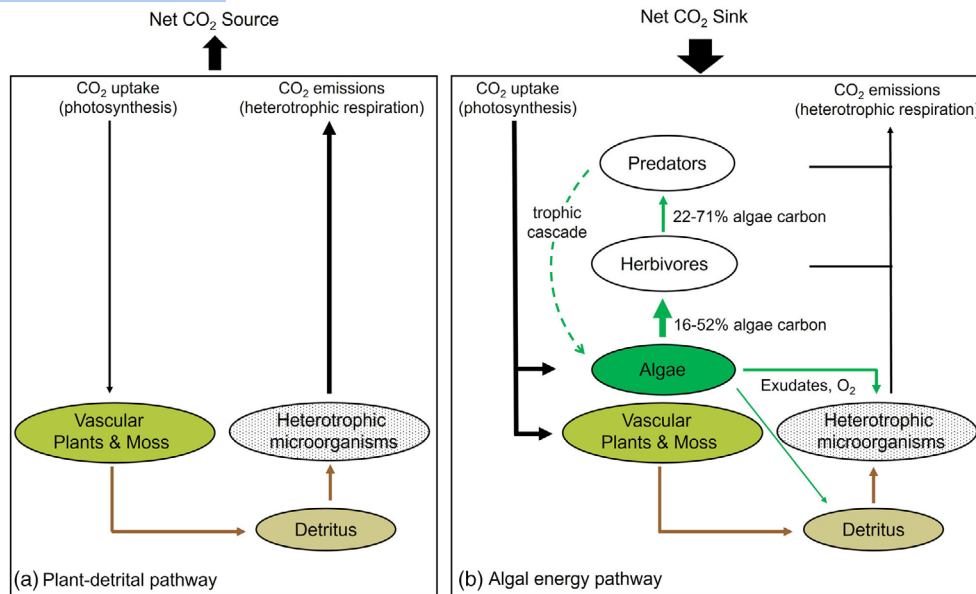


FIGURE 1 Conceptual diagram of energy flow through (a) plant-detrital (brown arrows) and (b) algal (green arrows) pathways. Solid arrows represent carbon flux between trophic compartments and the uptake of CO₂ by photosynthesis and release of CO₂ by heterotrophic respiration. Arrow thickness represents the magnitude of energy transfer or CO₂ flux. Dashed arrows represent indirect effects of predators (e.g. trophic cascade) on carbon storage. In a strictly plant-detrital pathway (a), energy flow is restricted by recalcitrant organic matter and carbon dioxide emissions from heterotrophic respiration exceed carbon uptake by plants. By comparison, in an algal energy pathway (b), algae support an animal food web that would not otherwise persist while also providing a labile source of carbon to heterotrophic microbes via exudates. While labile carbon can stimulate microbial decomposition, the presence of a trophic cascade releases algal production from top-down regulation, resulting in carbon dioxide uptake that exceeds carbon dioxide emissions via respiration.

et al., 1960; Moore et al., 2004; Vannote et al., 1980). Traditionally, wetlands have been considered brown energy pathways owing to plant litter being the primary source of organic matter available to heterotrophs (Batzer et al., 2006; van Duinen et al., 2013). This material is often recalcitrant in nature, making it a potential rate-limiting step for the propagation of energy in wetlands (Figure 1a). Nevertheless, the wetland literature is dominated by investigations into below-ground (i.e. brown) energy flow and the influence of plant litter on microbial-mediated biogeochemical cycling (Buttler et al., 2023; Robroek et al., 2015; Waldrop et al., 2012). In recent years, the importance of algae and other phototrophic microbes has become more apparent in wetlands (Gaiser, 2024; Hamard, Céréghino, et al., 2021; Jassey, Hamard, et al., 2022; Rober et al., 2014) and their role as a green energy pathway (Figure 1b) in northern wetlands appears to be increasing with processes associated with ongoing climate change (Ferguson et al., 2021; Wyatt & Turetsky, 2015). In this synthesis, we highlight the importance of microalgae as a basal resource for energy transfer in northern boreal wetlands, with a focus on fen peatlands where the future energy budget has implications for the global carbon cycle (Figure 1).

Peatlands are widespread across the boreal landscape (Kolka et al., 2018) and store large amounts of terrestrial carbon that is susceptible to being lost in a changing climate (Loisel et al., 2021; Yu, 2012). Like other wetlands, the hydrology of northern peatlands tends to be episodic, having both wet and dry stages that can occur across space (Hamard, Küttim, et al., 2021) or at a single

location at different points in time (Euskirchen et al., 2020). For the most part, studies of peatland ecology have focused on the dry stage where plants and associated detritus (i.e. the brown energy pathway) are considered the primary source of energy available for heterotrophs. Much of this plant material consists of mosses which are not easily broken down by heterotrophs, leading to the long-term accumulation of organic matter as peat (Rydin & Jeglum, 2013). While this paradigm is considered a defining feature of dry conditions, it does not fully represent periods of time when peatlands are inundated with water. Under these conditions, an aquatic biofilm develops on peat surface layers with the potential to shift the energy pathway to phototrophic microbes which sequester carbon but also have a greater potential for caloric uptake by heterotrophs (Figure 2; Crenier et al., 2017; Guo et al., 2016). The future of northern peatlands as a sink for CO₂ is uncertain and will depend largely on the nature of 'new' organic matter entering peatlands in conditions associated with future climate change, which may include expanded periods of surface water inundation (Fofana et al., 2022; Wickland et al., 2018).

Regular patterns of inundation frequency and duration (i.e. hydrologic regime) play a critical role in regulating community structure in aquatic ecosystems (Arias-Real et al., 2024; McMeans et al., 2019). While boreal peatlands are naturally dynamic ecosystems characterized by extreme fluctuations in temperature, daylight and hydrologic regime, these events tend to be seasonally recurring. More recently, ongoing climate change in northern regions has resulted in pronounced increases in growing season length, unprecedented

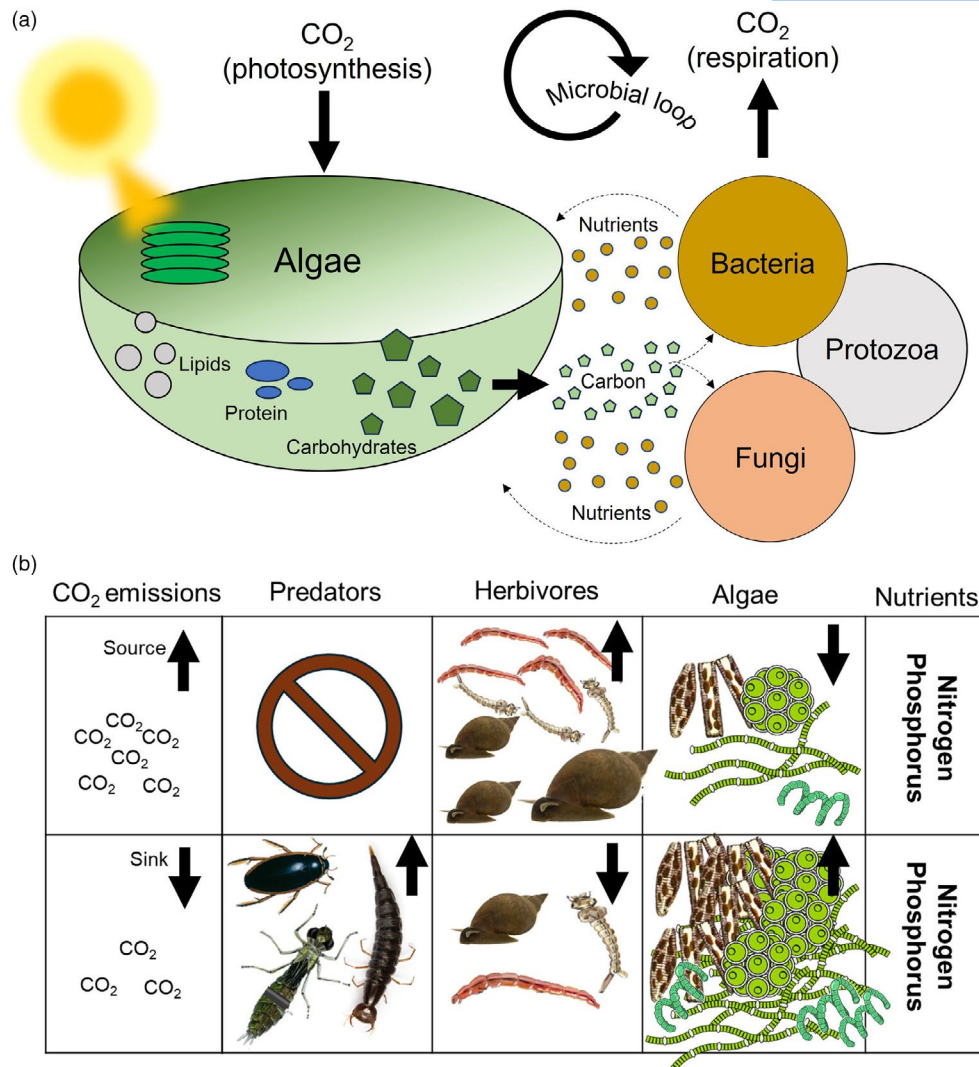


FIGURE 2 The algal energy pathway. Photosynthetic carbon fixation by microbial photoautotrophs (i.e. algae) sustains heterotrophic organisms and the propagation of energy through ecosystems. (a) Phototrophic microbes sequester carbon dioxide, but a portion of fixed carbon is released as simple carbohydrates that support heterotrophic metabolism and thereby enhance energy flow through the microbial loop. (b) Algal energy also moves up the food web through herbivores and predators, which contribute to ecosystem carbon exchange. Trophic dynamics can determine the extent to which decomposition associated with nutrient enrichment is translated into greater CO₂ emissions.

rates of warming and variable hydrology (Rantanen et al., 2022; Woodward et al., 2016). Warming in interior Alaska has increased the frequency of drought associated with evapotranspiration (Roach et al., 2011) while precipitation anomalies and changing run-off patterns associated with permafrost degradation (Douglas et al., 2020; Euskirchen et al., 2020) have increased flooding and the extent of open water areas (Jorgenson et al., 2001; Lara et al., 2016). Although nutrient levels are typically low in northern peatlands owing to slow rates of nutrient mineralization (Wieder, 2006), biogeochemical cycling is generally enhanced at the interface of distinct wet and dry stages (Bernhardt et al., 2017; McClain et al., 2003). More dynamic hydrologic conditions along with permafrost thaw are expected to increase low nutrient levels in open water bodies across the boreal landscape (Tank et al., 2020; Wickland et al., 2018) with yet uncertain consequences for carbon storage in peatlands.

2 | ENERGY FLOW THROUGH THE PEATLAND MICROBIAL LOOP WITH ENVIRONMENTAL CHANGE

Research in Alaskan fen peatlands has demonstrated that nutrient dynamics and biofilm metabolism during wet stages are strongly influenced by past hydrology (i.e. a legacy effect), especially the exposure to drought (Kane et al., 2021; Rober et al., 2013; Wyatt et al., 2024). Dry stages, which can occur in northern peatlands both within and among growing seasons (Euskirchen et al., 2024), increase organic matter decomposition (Boon, 2006), resulting in the release of nutrients from sediments into the overlying water column during inundation (DeColibus et al., 2017; Wyatt et al., 2012). Similar results have been reported in subtropical peatlands, where elevated levels of soluble nutrients promote algal biofilms growing attached to, and

in close association with, plants in the newly saturated photic zone (Gottlieb et al., 2005). Elevated algal photosynthesis can enhance carbon uptake by as much as 30% compared with conditions of more stable hydrology (Wyatt et al., 2012). Like plants, a portion of carbon fixed by algae is released directly into the water column as exudates (Bertilsson & Jones, 2003; Wyatt et al., 2014). The relevance of these compounds (e.g. simple carbohydrates) in the microbial loop (e.g. Halvorson, Francoeur, et al., 2019; Sanches et al., 2021; Wyatt & Rober, 2020) places algae in a key position to enhance energy flow through green pathways in northern peatlands (Figure 2a) where decomposition is often limited by recalcitrant organic matter (Moore & Basiliko, 2006).

Algae grow and form complex relationships with heterotrophic microorganisms on peat surface layers (Figure 2a), the nature of which is influenced by environmental conditions (Figure 3; Halvorson et al., 2020). Although producers and decomposers often compete for the same inorganic nutrients (Bratbak & Thingstad, 1985), both groups can coexist if nutrient levels surpass their combined energetic requirements (Currie & Kalff, 1984; Wyatt et al., 2019) or if decomposers are limited by organic carbon released by producers (Daufresne & Loreau, 2001). At least one of these conditions is met in the presence of elevated nutrient levels in northern fens because bacteria tend to increase along with algal production following inundation (DeColibus et al., 2017). However, bacteria do not always respond to nutrient enrichment in the absence of algae (i.e. in dark treatments) during bioassays (Rober et al., 2023; Wyatt & Turetsky, 2015). Owing to the recalcitrant nature of peatland dissolved organic matter (Hansen et al., 2016; Olefeldt et al., 2013), bacteria are often limited by labile carbon (Myers et al., 2021; Rober et al., 2023), and algae can alleviate this constraint through the release of exudates (Figure 3; Wyatt et al., 2012; Wyatt & Rober, 2020). In fact, periods of elevated algal productivity have a similar positive effect on heterotrophic metabolism as that of glucose enrichment (Wyatt & Turetsky, 2015). This suggests that bacteria are responding indirectly to elevated nutrient levels associated with more variable hydrology (DeColibus et al., 2017; Wyatt et al., 2012) and directly to an alternative green energy pathway provided by the algae.

Low temperatures across the boreal landscape exacerbate the effects of minimum nutrient levels on metabolic processes, which reduce the efficiency of nutrients for energy production (Markager et al., 1999). In contrast to other aquatic ecosystems in the region, where even relatively small increases in temperature tend to promote algal photosynthesis (Baulch et al., 2005; Demars et al., 2011), warming of surface waters alone does not typically stimulate algae or bacteria on peat surface layers (Gu & Wyatt, 2016; Wyatt et al., 2015). Disparities in results may be due to differences in background levels of nutrients among ecosystems, with fen peatlands typically among the most nutrient deplete (Wieder, 2006). When nutrient constraints are lifted, warming of $\geq 3^{\circ}\text{C}$ stimulates algal metabolism (Wyatt et al., 2015) and the transfer of energy to decomposers (Gu & Wyatt, 2016). Accordingly, algae in northern fens operate consistently with findings from the broader literature, demonstrating that growth rates are an exponential function of temperature in

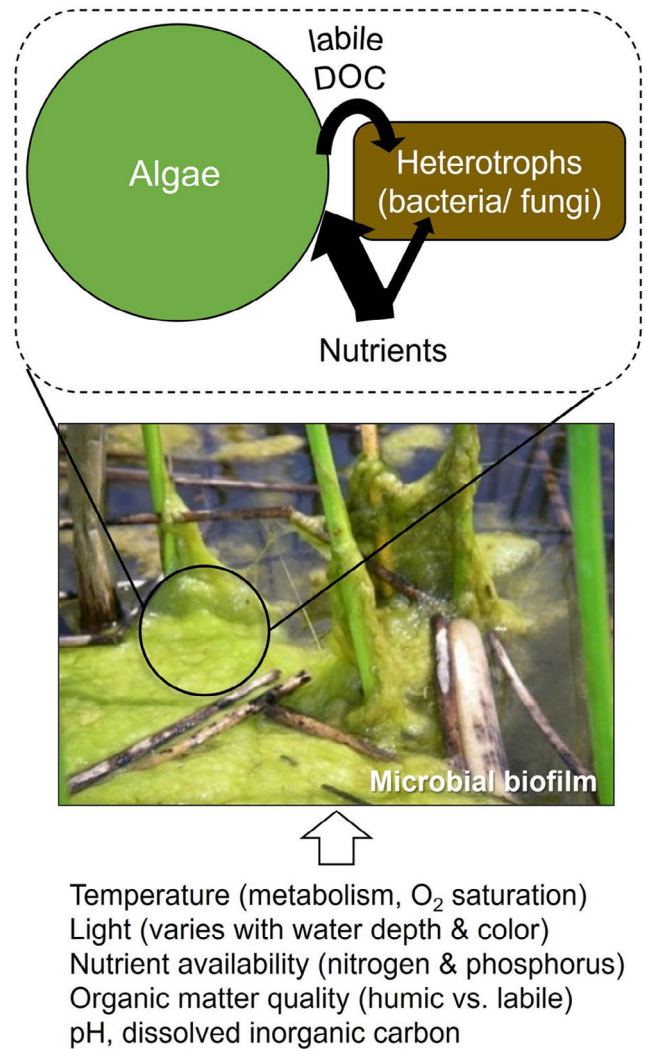


FIGURE 3 Environmental conditions influence the composition of the microbial mat. Within the microbial mat, algae (including cyanobacteria) produce organic compounds (i.e. exudates) during photosynthesis. Some of these compounds are released extracellularly where they are used as an energy source by the neighbouring heterotrophs (bacteria and fungi).

the presence of nutrient saturation (e.g. Bothwell, 1988; Goldman & Carpenter, 1974; Marcarelli & Wurtsbaugh, 2006). Owing to accelerated uptake of algal exudates, the combined effects of warming and nutrient enrichment enhance bacterial biomass by an additional 25% compared to nutrient enrichment alone (Gu & Wyatt, 2016; Wyatt et al., 2015; Wyatt & Rober, 2020). Therefore, current energetic restrictions on ecosystem metabolism driven by microbes may be poised for a rapid response to increased nutrient availability associated with a warmer climate in northern peatlands (Hamard et al., 2025; Le Geay et al., 2024).

The magnitude of energy transfer in a warmer, more nutrient-rich environment may depend on concurrent changes in the physical aspects of northern peatlands. Northern peatlands have naturally dark water, and light attenuation is a possible limiting factor even in relatively shallow waters owing to high levels of

dissolved organic matter and the presence of humic substances (Cory & Kling, 2018; Wickland et al., 2007). These conditions are expected to be exacerbated in the future owing to light attenuation associated with elevated levels of dissolved organic matter in surface waters (Frey & Smith, 2005; Rieb et al., 2024). Experiments across a gradient of light attenuation show that all positive effects of nutrient enrichment and the synergistic effects of nutrients and warming on algal photosynthesis are lost at $\leq 30\%$ ambient light (below $125 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Gu & Wyatt, 2016). Similar results have been reported in lotic studies showing that algal photosynthesis is limited by light availability at levels less than $100 \mu\text{mol m}^{-2} \text{s}^{-1}$, even with saturating nutrient supplies (Hill et al., 1995; Rier et al., 2006). Despite not using light directly, heterotrophic bacteria decline with light attenuation owing to their dependence on algae as an energy source (Gu & Wyatt, 2016). Within a predictive context, biofilm development in northern peatlands will become limited by light attenuation if current levels of dissolved organic matter (of approximately 28 mg L^{-1}) are doubled or if the average maximum water depth of approximately 16 cm increases to >45 cm (Wyatt et al., 2024)—circumstances that are becoming increasingly common in the region following the spring snowmelt (Euskirchen et al., 2020, 2024).

In addition to being directly affected by the optical properties of humic organic matter, algae, through the release of secondary metabolites, can affect the reactivity and chemical composition of organic matter through both positive and negative priming (Halvorson, Barry, et al., 2019; Wyatt & Rober, 2020). For instance, when exudates released by algae mix with fen organic matter, microbial degradation of the mixture solution proceeds at a faster rate than expected (i.e. based on the average of individual substrates) by as much as 10%, and the magnitude of this effect increases to more than 15% with warming (Wyatt & Rober, 2020). In some cases, biodegradation in the mixture solution can even surpass that of either algal exudates or fen organic matter alone (Wyatt & Rober, 2020), indicating complementary metabolism among decomposers (Farjalla et al., 2009; Loreau, 1998). Since complementary metabolism often involves degradation by extracellular enzymes (Münster & De Haan, 1998), it is widely considered a pathway for the priming effect, where recalcitrant organic matter is mineralized following the addition of more labile sources (Bianchi & Ward, 2019; Guenet et al., 2010). Similar results have been reported from temperate ecosystems, including wetlands and rivers (Halvorson, Francoeur, et al., 2019; Sanches et al., 2021), where organic matter reactivity can be accelerated by the addition of substrates from algae. Other mechanisms, such as negative priming, may also influence the rates of recalcitrant organic matter decomposition and mineralization whereby algae decouple microbial decay activity from litter decomposition (Halvorson, Barry, et al., 2019). In either case, synergistic effects in mixture solutions result in greater aromaticity than expected based on values of individual substrates, with possible implications for optical properties (i.e. darker water) that could feedback on light attenuation (Rieb et al., 2024). These findings move past simply showing that exudates from algal sources are an important energy

source for decomposers and present an alternative energy pathway for heterotrophic consumers to break down and transform organic matter in northern peatlands.

3 | ENERGY FLOW TO HIGHER TROPHIC LEVELS

Periods of elevated algal production result in basal resources available for energy transfer to higher trophic levels in northern peatlands (Figure 2). In conditions of low nutrient availability, algal production is typically low and higher trophic levels are nearly absent from peatland surface waters (Ferguson et al., 2021; Rober et al., 2011). However, a diverse community of aquatic consumers develops along with algae in response to increased nutrient availability associated with variable hydroperiods (DeColibus et al., 2017). Elevated algal production contributes to herbivore abundance directly as a food source and indirectly by promoting heterotrophic bacteria within the biofilm (which are also consumed by grazers; Ferguson et al., 2021; Rober et al., 2022). Consistent with food web theory (e.g. Hansson, 1992), an increase in basal resources allows predators to invade the system, which increases in abundance along with herbivores (DeColibus et al., 2017; Ferguson et al., 2021). Stable isotope analysis (^{13}C and ^{15}N) shows that approximately 79% of energy transferred to primary consumers and 82% of the energy transferred from primary consumers to predators in northern peatlands can be attributed to algal sources (DeColibus et al., 2017). A similar trend emerges across a range of northern peatlands where algal biofilm contributes more to consumer diet over the growing season (71%–76% in a rich fen, 78%–81% in a moderate fen and 20%–65% in a poor fen; \bar{x} = 65% average across all sites) than all other possible sources of carbon combined (bryophytes, vascular plants and detritus contribute less than 7% on average; Ferguson et al., 2021). This ecosystem, where secondary production is generally considered to be based on plant detrital pathways, relies primarily on green energy pathways (Figure 1b), opening the possibility for animal regulation of the peatland carbon cycle with wetter conditions associated with climate change. More frequent or extended periods of drought may restrict energy flow to higher trophic levels in favour of the microbial food web (e.g. protozoans; Barel et al., 2023; Gilbert et al., 1998; Jassey et al., 2023).

4 | THE ROLE OF ALGAE IN ECOSYSTEM CO_2 FLUX

Variability in CO_2 flux between wet and dry stages can be attributed to the availability of algae on peat surface layers (Kane et al., 2021), where net CO_2 uptake reflects an imbalance between producers and decomposers in favour of autotrophy (Wyatt et al., 2024). The predominance of an autotrophic over a heterotrophic biofilm can be facilitated by elevated nutrient levels associated with variable hydrology (DeColibus et al., 2017; Wyatt et al., 2012) and by

plant leachates entering the organic matter pool following senescence (Rober et al., 2023; Wyatt et al., 2024). A range of peatland plants release organic matter into the water column during active growth and following senescence, some of which are rich in carbohydrates (Farjalla et al., 2009; Robroek et al., 2016). A supply of fresh organic carbon from plants has the potential to shift the biofilm in favour of heterotrophy by competitively excluding algae. Instead, the nutrient content of peatland plants—more so than carbon quality—regulates biofilm composition (Rober et al., 2023). By alleviating nutrient limitation of the algae, plant leachates shift the biofilm in favour of autotrophy and reduce CO₂ emissions (Rober et al., 2023; Wyatt et al., 2024). The peatland literature is dominated by studies that focus on nutrients as facilitators of decomposition and CO₂ emissions (Aerts et al., 1995; Bragazza et al., 2006), but on wet peat surfaces, nutrient enrichment can promote CO₂ uptake by releasing constraints on algal photosynthesis (Rober et al., 2023). In dark water without a counterbalance from algal photosynthesis, plant leachates do in fact promote a heterotrophic biofilm, resulting in a release of CO₂ (Wyatt et al., 2024). Conditions that support an autotrophic biofilm tend to operate as a net sink of CO₂, taking up as much as $29.0 \pm 6.02 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ (Wyatt et al., 2024). The same site can switch to a CO₂ source when conditions favour a heterotrophic biofilm, releasing on average $8.65 \pm 0.90 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ to the atmosphere (Wyatt et al., 2024).

The aquatic food web that develops in response to the algal-energy pathway also contributes to the carbon sink potential (i.e. net ecosystem carbon exchange) of northern peatland ecosystems (Figure 2b). More specifically, trophic dynamics can determine the extent to which decomposition associated with nutrient enrichment is translated into greater CO₂ emissions from peat surface layers (Rober et al., 2022; Wyatt et al., 2021). When net ecosystem exchange (NEE) is compared on an annual basis between treatments without nutrient additions ($\text{NEE} > 400 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$) and where nutrients were present but algae were removed by grazing ($\text{NEE} > 700 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$), nutrient enrichment results in a net release of $300 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ without a counterbalance from algal photosynthesis (Wyatt et al., 2021). Predators, by releasing algae from grazing pressure in a trophic cascade, can indirectly reduce NEE to approximately $200 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$, which mitigates CO₂ emissions associated with nutrient inputs. Trophic interactions have little to no effect on CO₂ flux under ambient conditions, as nutrient constraints on biofilm development restrict energy transfer to higher trophic levels. The net reduction in carbon flux of $500 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ highlights the importance of algae for carbon sequestration in northern peatlands. Considering that open water areas of northern peatlands release $23\text{--}419 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ (Pelletier et al., 2014; Waddington & Roulet, 2000), trophic interactions can mitigate CO₂ emissions and determine whether an individual peatland is a carbon source or sink following nutrient enrichment. The ability for animals to regulate ecosystem carbon cycling is not limited to peatlands but appears to be a growing trend across both terrestrial and aquatic ecosystems (Nelson et al., 2023; Schmitz & Leroux, 2020).

5 | FUTURE DIRECTIONS

Peatlands located within floodplain landscapes have largely intermittent hydrology, and the paucity of information on these ecosystems may reflect the inherent difficulty of studying such environments (Arias-Real et al., 2024). While studies have looked at microhabitat variability across space (e.g. dry to wet gradient) that include static peatland pools (Hamard, Küttim, et al., 2021; van Duinen et al., 2013; Vesterinen et al., 2016), work described in this synthesis has focused on many of the same fen locations at different points in time. Only in the presence of a long-term research site is it possible to access hydrologic data from a single location during both wet and dry stages. This is notable because many of the findings presented here hinge on the knowledge of past conditions in shaping nutrient cycling and microbial communities during periods of inundation. Without knowledge of the previous growing season (i.e. a drought period), it would be difficult to ascertain the mechanisms controlling biofilm development during periods of inundation. This highlights the need to study both wet and dry stages to capture a complete picture of carbon cycling in northern fens, even if wet periods are the primary interest.

Trace gas measurements presented in this synthesis show that hydrologic legacy affects autotrophic biofilm production with direct effects on ecosystem carbon flux (Kane et al., 2021; Wyatt et al., 2024). While these findings are illuminating, they only include estimates of carbon uptake by autotrophic microbes in a fen during the wet stage (Rober et al., 2023; Wyatt et al., 2021, 2024). This does not account for phototrophic carbon uptake during the dry stage or how these processes might differ in other peatland types (e.g. bogs). Research during dry stages has largely focused on heterotrophic microorganisms and their role in decomposition and soil biogeochemical cycles (e.g. Lamit et al., 2021; Seward et al., 2020; Tedersoo et al., 2014; Waldrop et al., 2023). However, algae can be diverse and abundant in dry environments (Cano-Díaz et al., 2020; Oliverio et al., 2020; Schmidt et al., 2016) where they contribute to CO₂ uptake through photosynthesis, similar to that of plants (Jassey, Walcker, et al., 2022; Jassey, Hamard, et al., 2022). However, since algae often constitute a smaller proportion of the total microbiome biomass compared to heterotrophic microorganisms in terrestrial ecosystems, microbial photosynthesis remains overlooked, especially in carbon-accumulating systems such as peatlands (Jassey, Walcker, et al., 2022; Jassey, Hamard, et al., 2022).

It is not yet clear how environmental conditions expected with climate change will regulate the contribution of algae to CO₂ uptake during dry stages. A combination of experimental observations and biogeochemical modelling has demonstrated that warmer temperatures will increase microbial photosynthesis on dry surfaces by an average of 68% across seasons, which could offset about 20% of peatland CO₂ emissions projected under climate change (Hamard et al., 2025). Soil moisture is inherently linked to temperature, and recent studies have shown that moisture content is a key driver of microbial carbon cycling (Hamard, Céréghino, et al., 2021; Hamard, Küttim, et al., 2021; Jassey, Walcker, et al., 2022; Jassey, Hamard, et al., 2022;

Reczuga et al., 2020). Studies conducted across spatial transitions in microhabitats (e.g. from dry surfaces such as hummocks to permanent deep pools) indicate that microbial carbon uptake decreases with moisture content (Hamard, Küttim, et al., 2021; Nelson et al., 2023) while studies conducted across a temporal moisture gradient resulting from fluctuating water levels at a single fen location show the opposite trend (Figure 4a,b). These studies have also revealed that algal biomass (measured as chlorophyll *a*) is related to plant health (measured as photosynthetic capacity; Figure 4c), suggesting that temporal shifts in soil moisture may be influencing carbon cycling in unexpected ways. Given that algae and other photosynthetic microbes, together

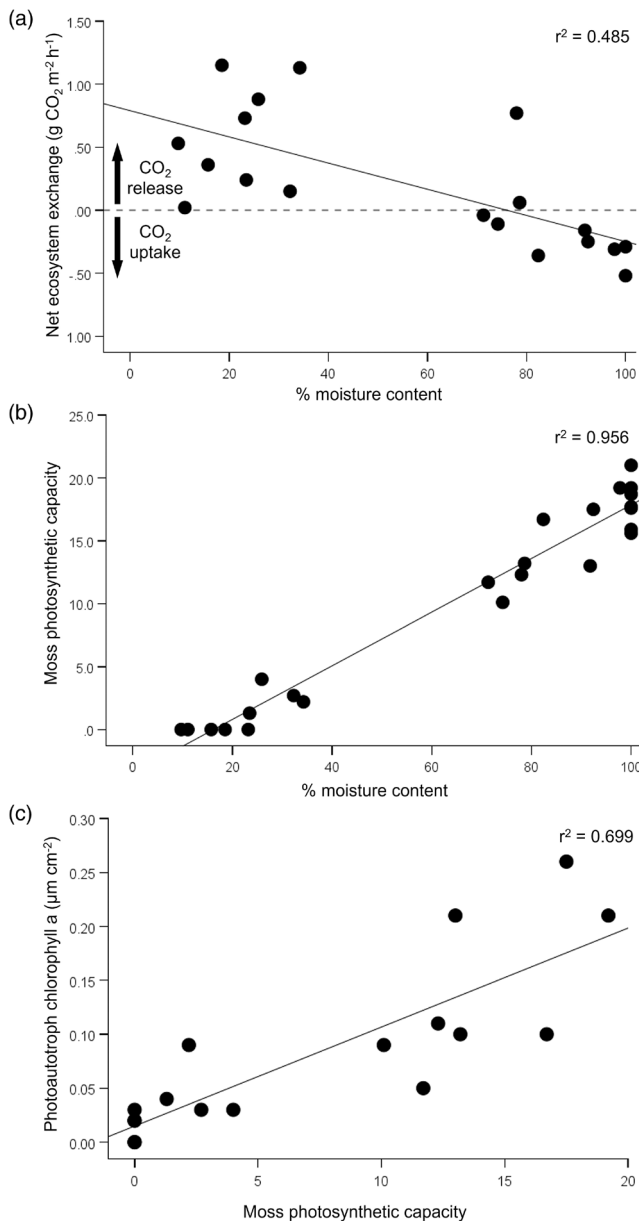


FIGURE 4 (a) An increase in carbon uptake along a moss-moisture gradient, (b) an increase in moss health (measured as electron transport rate) with increasing moisture content and (c) an increase in microbial photoautotroph biomass (measured as chlorophyll *a*) with increasing moss health.

with heterotrophic microorganisms, remain an integral part of the microbiome on dry surfaces (Hamard, Küttim, et al., 2021), the role of algae in peatlands with variable hydroperiods is likely underestimated. Consequently, our current understanding of peatland carbon dynamics still lacks a significant piece of the puzzle.

Species composition is also important for determining the flux and transformation of carbon and nutrients in peatland environments (Ernakovich et al., 2022; Jassey, Hamard, et al., 2022). Yet, current efforts to describe peatland microbial diversity have focused on the below-ground microbial community (bacteria, archaea, fungi) (Lamit et al., 2021; Seward et al., 2020; Waldrop et al., 2023) and have largely ignored the above-ground microbiome. Research has shown that microbial interactions in above-ground communities can influence below-ground carbon storage through changes in the form and availability of energy inputs into the microbial loop (Jassey, Hamard, et al., 2022; Schmidt et al., 2016; Schmitz & Leroux, 2020). Moreover, there is growing evidence from other ecosystems that bacterial and fungal community structure differs in the presence or absence of algae (Miura & Urabe, 2017; Seballos et al., 2020) and that interactions with algae influence gene expression and subsequently trait-mediated metabolic functions within the heterotrophic community (Linz et al., 2020). Changes in gene expression associated with photosynthesis may be of particular interest within aquatic biofilms given that photosynthetic and heterotrophic members of the biofilm are intricately linked through the exchange of resources (Figure 2a; Halvorson et al., 2020; Wyatt et al., 2019; Wyatt & Rober, 2020).

6 | CONCLUSIONS

Peatlands are among the most productive and valuable ecosystems, and they are particularly important to the Earth's climate system when they occur in high-latitude regions. Peatlands in boreal and subarctic regions contain as much as 30% of the world's soil carbon, but rising temperatures associated with global climate change are expected to stimulate decomposition and release soil carbon as CO₂, which could serve as positive feedback on global warming. Traditionally, plants have been the focus of study in northern peatlands, owing in part to the large amount of carbon stored by the litter of these organisms (Wieder, 2006). However, recent studies have shown that microbial photoautotrophs, including algae, can account for 30% or more of peatland primary productivity (Hamard, Céréghino, et al., 2021; Wyatt et al., 2012). Owing to changing environmental conditions, including the expansion of open water areas associated with precipitation anomalies, this amount is expected to increase, resulting in a shift in the active mode of peatland primary production, from plants to algae during periods of inundation. Understanding how this alternative mode of primary production will influence peatland ecology and future carbon storage is a primary goal of this synthesis.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception, design and writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

None declared.

DATA AVAILABILITY STATEMENT

Data from this manuscript are available at <http://www.lter.uaf.edu/data/data-detail/id/774> (Wyatt, 2020).

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